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SYNOPSIS OF THE GENUS *ONOSMODIUM* (BORAGINACEAE)

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ABSTRACT

A taxonomic study of *Onosmodium* (Boraginaceae) is rendered. The genus is confined to México, the U.S.A., and closely adjacent Canada Seven species of *Onosmodium* are recognized, as follows: a widespread *O. bejariense* [with four morphogeographical varieties: var. *bejariense*; var. hispidissimum (Mack.) B.L. Turner, *comb. nov.*; var. occidentale (Mack.) B.L. Turner, *comb. nov.*; and var. subsetosum (Mack. & Bush) B.L. Turner, *comb. nov.*]; *O. dodrantale*, confined to México; *O. helleri*, confined to Texas; *O. molle*, a localized cedar glades endemic of central Tennessee and closely adjacent Alabama and Kentucky; *O. oaxacanum*, confined to México; *O. virginianum*, widespread in the eastern U.S.A.; and *O. unicum*, confined to México. A key to all of these taxa is provided, along with distributional maps.

KEY WORDS: Boraginaceae, *Onosmodium*, taxonomy

The present study was occasioned by the author's attempt to annotate approximately 5000 sheets of the genera *Lasiarrhenum*, *Macromeria*, and *Onosmodium* on loan to TEX for doctoral work by Ms. H.-G. Kim. She subsequently switched her doctoral focus, with my encouragement, to DNA studies on the Compositae working in Dr. Bob Jansen's laboratory, thus precluding (timewise) any opportunity for the kind of study which I have provided here. My taxonomic concepts of these several genera are essentially the same as those used in my prior treatments of various genera of the families Asteraceae, Leguminosae, and Lamiaceae, especially as regards the treatment of infraspecific categories.

MacKenzie (1906) provided an early inclusive treatment of *Onosmodium* for the U.S.A., recognizing seven species. Macbride (1917) and Johnston (1924) provided additional insight by expanding upon the observations of earlier authors. Johnston (1954a, b), in particular, clarified the generic limits of *Onosmodium* and clearly contrasted and delineated the generic limits of the closely

related *Lasiarrhenum*, *Lithospermum*, *Macromeria*, and *Perittostema*. Turner (1994) combined *Lasiarrhenum* and *Perittostema* and subsequently provided an overview of the largely Mexican genus *Macromeria* (Turner 1995).

Onosmodium was not treated in detail by Johnston (1954a, b), but Das (1965) provided an unpublished taxonomic account of the genus. The work of Das was reasonably sound, but his familiarity with taxa in the field was relatively limited.

As treated below, *Onosmodium* is a small genus of seven species, four of these mostly confined to the U.S.A., and three to México. Only one species, *O. bejariense*, is treated as having meaningful infraspecific categories; within this, four intergrading regional varieties are recognized.

KEY TO SPECIES OF *ONOSMODIUM*

1. Vestiture of stem, at least in part, composed of glandular trichomes; México. ..... *O. unicum*

1. Vestiture of stem without glandular trichomes. .....(2)

2. Low herbs 15-30 cm high; Mexican species. .....(3)

2. Tall herbs 30-80 cm high; U.S.A. species. .....(4)

3. Inflorescence short, 3-10 flowered; corolla tube glabrous within or nearly so; northeastern México. ..... *O. dodrantale*

3. Inflorescence elongate, 20-flowered or more; corolla tube pubescent within with numerous elongate hairs; Oaxaca. ..... *O. oaxacanum*

4. Pedicels of flowers, at anthesis and later, mostly 5-15 mm long; Edwards Plateau region of southcentral Texas. ..... *O. helleri*

4. Pedicels of flowers, at anthesis and later, mostly 0.5-5.0 mm long. . . ..(5)

5. Lobes of corolla yellowish, linear-lanceolate to narrowly triangular, mostly 3-4 times as long as wide; Atlantic and Gulf Coastal plains from Massachusetts to eastern Louisiana. ..... *O. virginianum*

5. Lobes of corolla greenish or whitish, variously deltoid or broadly triangular, mostly 1-2(-3) times as long as wide; more inland regions of the U.S.A. .....(6)

6. Leaves densely and uniformly appressed-pubescent on both surfaces, the whole plant ashy-white (rarely not ashy-white, but hairs otherwise all appressed); cedar glades of central Tennessee and closely adjacent Kentucky and Alabama. ..... *O. molle*

6. Leaves not pubescent as described in the above, the leaf vestiture nearly always with spreading or ascending hairs of two or more kinds; widespread but not in the cedar glades of Tennessee or closely adjacent Alabama and Kentucky. ..... *O. bejariense*

ONOSMODIUM BEJARIENSE A. DC., *Prodr.* 10:70. 1846.

Perennial erect or ascending often suffruticose herbs mostly 40-110 cm high, the stems arising from crowns of ligneous or woody roots. Midstems glabrous to densely appressed-pubescent or pilose, often with a mixed array of both appressed and pilose hairs. Midstem leaves lanceolate, oblanceolate or variously elliptical, sessile or nearly so, 6-12 cm long, 2-4 cm wide, variously pubescent. Flowers 10 or more in terminal or branched racemes. Calyces 4-9 mm long, the lobes linear lanceolate to oblanceolate, 0.7-1.5 mm wide. Larger corollas, whitish or greenish-white, mostly 17-20 mm long; tubes 14-16 mm long; lobes deltoid, 2.4-4.5 mm long, 1.4-3.0 mm wide, 1-2 times as long as wide (rarely not), glabrous within, pubescent without. Stamens extending to about the base of the corolla lobes; anthers 2-4 mm long (including the terminal, often recurved mucro). Mature styles extending from the corolla for 5-25 mm. Nutlets mostly 3-5 mm long, 2.4-3.5 mm wide, tapering to the base, or constricted.

This is a widespread highly variable species occurring throughout most of the central and eastern U.S.A. My concept of the taxon is essentially the same as that of Cronquist (1959), Das (1965), Cochrane (1976), and Kaul (1986), except that I exclude from it *Onosmodium molle* Michx. which I recognize as a distinct species (for reasons elaborated upon in my discussion of the latter). With the removal of *O. molle*, the earliest name for the species (*s.l.*) is *O. bejariense*, typified by material from southcentral Texas. Most of the material of the four varieties so recognized can be identified by the key presented below, but in regions of near sympatry or "overlap," intermediates between the more typical forms often abound, as nicely documented by the study of Cochrane, who treated the infraspecific taxa as subspecies. The subspecific categories may be applied to the nomenclature I am proposing in the following manner:

1. *Onosmodium bejariense* A. DC. subspecies *bejariense* (authority automatic)
   a. *Onosmodium bejariense* A. DC. var. *bejariense*
   b. *Onosmodium bejariense* A. DC. var. *occidentale* (Mack.) B.L. Turner
   c. *Onosmodium bejariense* A. DC. var. *hispidissimum* (Mack.) B.L. Turner
2. *Onosmodium bejariense* A. DC. subspecies *subsetosum* (Mack. & Bush) Cochrane

a. *Onosmodium bejariense* A. DC. var. *subsetosum* (Mack. & Bush) B.L. Turner

Das (1965) presented a reasonably well-constructed key to the five varieties (including *Onosmodium mollis*), with much emphasis upon corolla lobes and nutlet shape, and Cochrane (1976) provided a perceptive key (as subspecies) to the varieties *hispidissimum* and *occidentale* in Wisconsin, emphasizing nutlet shape, but noting that "some specimens show overlapping or recombining characters so as to appear variously intermediate between the subspecies". Similar statements by others have been made for this complex as it occurs in Illinois, Missouri, and perhaps elsewhere.

KEY TO VARIETIES OF *O. BEJARIENSE*

1. Stems mostly glabrous below the branches of the inflorescence; central and southern Missouri and closely adjacent Arkansas and Oklahoma. .... var. *subsetosum*

1. Stems clearly and persistently pubescent below the branches of the inflorescence; widespread. .....(2)

2. Corollas mostly 6-10 mm long; nutlets mostly flared at the base; interior regions of northeastern U.S.A. (and closely adjacent Canada) from New Hampshire south to the Carolinas and westwards to the eastern portions of Minnesota, Illinois, Missouri, and closely adjacent Canada. .....var. *hispidissimum*

2. Corollas mostly 11-20 mm long, nutlets mostly tapered to the base; southcentral U.S.A. mainly in grassland regions from Canada to southcentral Texas. .....(3)

3. Midstem hairs widely spreading, the vestiture mostly 2-4 mm high; nutlets mostly 3-4 mm long; southcentral U.S.A. from Oklahoma and Arkansas south to southern Texas. ..... var. *bejariense*

3. Midstem hairs appressed or ascending, the vestiture mostly 1-2 mm high; nutlets mostly 4-5 mm long; northcentral U.S.A. from northeastern New Mexico and western Texas north to Canada. ..... var. *occidentale*

ONOSMODIUM BEJARIENSE A. DC. var. *BEJARIENSE*

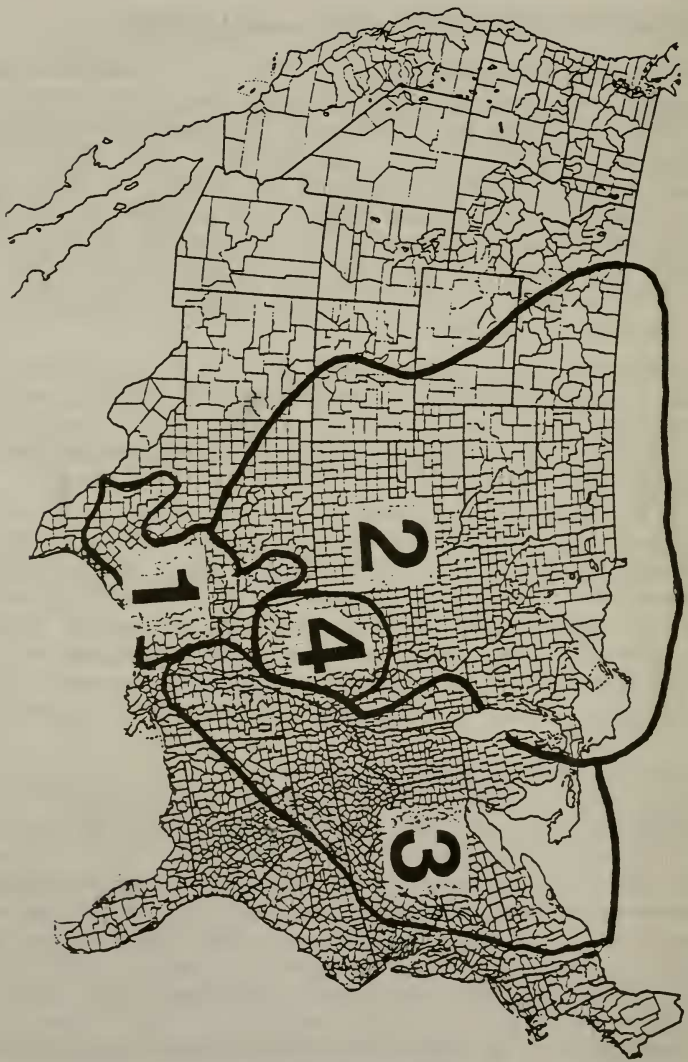
Onosmodium bejariense A. DC., *Prodr.* 10:70. 1846. *Onosmodium molle* Michx. var. *bejariense* (A. DC.) Cronquist, *Vasc. Pl. Pac. N.W.* 4:234. 1959. *Onosmodium molle* Michx. subsp. *bejariense* (A. DC.) Cochrane, Michigan Bot. 15:104. 1976. TYPE: U.S.A. Texas: "Bejar ad Rio de la Trinidad" [probably in present day Madison Co., Texas, along the Trinity River at Robbins Crossing or Ferry, which was established in 1821 as the Paso Thomas crossing of the old San Antonio and La Bahia Roads over the Trinity River; *cf.* Geiser 1937], May 1828, *J.L. Berlandier 1681* (HOLOTYPE: G-DC; Fragment isotype: GH!; Photoisotypes: F!,GH!,MICH!).

My delineation of var. *bejariense* differs from that of Das (1965) in my inclusion of numerous specimens from northcentral Texas, Oklahoma, Arkansas, and occasional plants from Louisiana (cited below) which he would include in his concept of ssp. *occidentale*, to judge from his distributional map and specimens cited.

The var. *bejariense* is very closely related to var. *occidentale*, the two differing mostly by pubescence and nutlet size, the stems of the former with longer-spreading hairs and the nutlets generally smaller. The two varieties intergrade over a broad area of Oklahoma and Kansas. Das (1965) followed Cronquist in treating *bejariense* as a variety of *Onosmodium molle*. Unfortunately, Correll & Johnston (1970) in their treatment of *Onosmodium* for Texas, maintained *O. bejariense*, *O. hispidissimum* Mack., and *O. occidentale* Mack. as distinct species, following the early treatments provided by Johnston (1924, 1967).

Since my delineation of var. *bejariense* differs from that of Das, especially as to geographical distribution, I have included below an abbreviated list of the specimens examined in the present study. It should be emphasized that nearly all of the plants of *Onosmodium bejariense* from Texas (Figures 1-4) belong to var. *bejariense*, there being only two Texas collections of var. *occidentale* known to me, one from Wichita Co. (*Tharp s.n.* [TEX]) – mapped by Das as var. *bejariense*, and the other from Tarrant Co. (*Ruth 98* [GH]), although the latter is listed from Denton Co. on label data on a specimen at US!. Actually, both collections approach var. *bejariense* in stem-pubescence, but overall they seem closest to var. *occidentale*.

REPRESENTATIVE SPECIMENS: U.S.A. Arkansas: Lincoln Co.: *Demaree 2260* (OKLA,UC). Little River Co.: *Johnson 617* (MICH). Sevier Co.: *Demaree 64944* (MICH). Oklahoma: Choctaw Co.: *Trott s.n.* (OSU). Mayes Co.: *Wallis 3346* (OKLA). Payne Co.: *Powers 213* (OKLA). Pontotoc Co.: *Robbins 2802* (UC). Tulsa Co.: *Clark 310* (OSU). Louisiana: Calcasieu Parish: *Palmer 7698* (CAS). Cameron Parish: *Givens 4739* (MICH). Natchitoches Parish: *Palmer 7467* (CAS). Winn Parish: *Urbatsch 4477* (MICH).



Figures 1-4. General distribution of the varieties of *Onosmodium bejariense*: 1 - var. *bejariense*; 2 - var. *occidentale*; 3 - var. *hispidissimum*; and 4 - var. *subsetosum*. In regions of contact, intermediates between these morphogeographical taxa commonly occur.

Texas: Bell Co.: *Wolff 2825* (US). Bexar Co.: *Lundell 10268* (GH,LL,MICH). Brazoria Co.: *Jordan s.n.* (LL). Chambers Co.: *Traverse* (GH,TEX). Cherokee Co.: *Palmer 13347* (WIS). Collin Co.: *Lundell 9294* (LL). Colorado Co.: *Joor s.n.* (US). Comal Co.: *Lindheimer* (ARIZ,F,GH,NY,PH,TEX,UC,US). Dallas Co.: *Lundell 13637* (GH). Ellis Co.: *Cory 23385* (GH). Fannin Co.: *Correll 37305* (LL,NY). Fayette Co.: *Forshey s.n.* (US). Goliad Co.: *Williams 68* (PH,TEX). Gonzales Co.: *Ginsbarg 925* (F,TEX). Grimes Co.: *Massey 122* (LL). Harris Co.: *Fisher 462* (US). Hays Co.: *Johnson 495* (KANU,NY,TEX). Jackson Co.: *Palmer 9716* (CAS,US). Kendall Co.: *Smith 29557* (LL). Kimble Co.: *Palmer 10919* (CAS,US). Lamar Co.: *Correll 37507* (GH,LL,TEX). Live Oak Co.: *Correll 27055* (LL,TEX,UC). McLennan Co.: *Smith 1159* (KANU,TEX). Medina Co.: *Hamby 1699* (LL). Menard Co.: *Cory 24768* (KANU,GH). Polk Co.: *Orzell 10812* (TEX). Sabine Co.: *Carr 13110* (TEX). San Augustine Co.: *Palmer 7890* (CAS,NY,US). Tarrant Co.: *Ruth 216* (TEX). Tom Greene Co.: *Tweedy s.n.* (NY). Travis Co.: *York 46053* (GH,LL,TEX). Uvalde Co.: *Palmer 33647* (GH,NY,US). Victoria Co.: *Schwarz s.n.* (US). Walker Co.: *Dixon 394* (F,GH,WIS). Washington Co.: *Tharp s.n.* (GH,MICH,TEX,UC). Williamson Co.: *Whitehouse 19925* (OKLA). Wilson Co.: *Palmer 9193* (CAS,PH,US).

DISTRIBUTION (Figure 1) AND ECOLOGY: Southcentral Texas northwards to Oklahoma and eastwards to eastern Tennessee and Alabama, mostly in grasslands or forest openings in deep silty or silty-clay soils; flowering May-July.

ONOSMODIOM BEJARIENSE A. DC. VAR. HISPIDISSIMUM (Mack.) B.L. Turner, *comb. nov.* BASIONYM: *Onosmodium hispidissimum* Mack., Bull. Torrey Bot. Club 32:500. 1905. *Onosmodium molle* Michx. var. *hispidissimum* (Mack.) Cronquist, *Vasc. Pl. Pacific NW* 4:234. 1959. *Onosmodium molle* Michx. subsp. *hispidissimum* (Mack.) Boivin, Phytologia 22:372. 1972. TYPE: U.S.A. Indiana: Tippecanoe Co.: 4 mi sw of Lafayette, along Big Wea Creek, below Wabash railroad, 17 Jun 1941, *Charles M. Ek s.n.* (LECTOTYPE: NY!, selected by T. Barkley but first published here; Isolectotypes: CAS!,UC!).

Onosmodium hispidissimum Mack. var. *macrospermum* Mack. & Bush, Bull. Torrey Bot. Club 32:502. 1905. TYPE: U.S.A. Missouri: Jackson Co., Atherton, 7 Sep 1895, *Bush 363* (type material not located).

Cochrane (1976) unnecessarily proposed the combination *Onosmodium molle* subsp. *hispidissimum* (Mack.) Cochrane, this combination having been published by Boivin in 1972. Das (1965) thought var. *hispidissimum* to be based

upon *O. carolinianum* L. var. *molle* sensu A. Gray (1886), but the latter applies to *O. molle* Michx., Gray apparently intent on reducing the latter name to varietal status under *O. carolinianum* L. (= *O. virginianum* [L.] A. DC.).

The var. *hispidissimum* is widespread in the northeastern U.S.A., yet it is not especially well represented in herbaria, at least as compared with the variety *occidentale* with which it intergrades, as documented by Cochrane (1976) for Wisconsin. Var. *hispidissimum* superficially resembles var. *bejariense* but the latter is readily distinguished by its larger corollas (mostly 17-20 mm long vs. 6-10 mm long) and its mostly smaller nutlets which do not usually flare at the base. Most specimens of var. *hispidissimum* previously reported from the southeastern U.S.A. (Arkansas, Louisiana, Mississippi, and Alabama) are, in my opinion, considerably introgressed by var. *bejariense*. Indeed, it is probable that populations and/or individuals of *O. virginianum* in this region which have received the name var. *hirsutum* Mack. are the likely residuum of gene flow between ancestral populations of *O. bejariense* and *O. virginianum*.

REPRESENTATIVE SPECIMENS: These need not be cited here since the characters which mark typical elements of var. *hispidissimum* are fairly well-marked, and the specimens are mostly confined to the northeastern U.S.A. Nonetheless, there is considerable intergradation of this taxon into var. *occidentale* where the two come in contact (Figures 2-3), and with var. *bejariense* in the southeastern U.S.A., as noted above.

DISTRIBUTION (Figure 3) AND ECOLOGY: Eastern U.S.A. and closely adjacent Canada from Maine to North Carolina, and southeastwards to Louisiana and northwards to Wisconsin, usually occurring in shady areas in deep clay or upon stony banks; flowering June-July.

ONOSMODIUM BEJARIENSE A. DC. VAR. OCCIDENTALE (Mack.) B.L. Turner, *comb. nov.* BASIONYM: *Onosmodium occidentale* Mack., Bull. Torrey Bot. Club 32:502. 1905. *Onosmodium molle* Michx. var. *occidentale* (Mack.) I.M. Johnst., Contr. Gray Herb. n.s. 70:18. 1924. *Onosmodium molle* Michx. subsp. *occidentale* (Mack.) Cochrane, Michigan Bot. 15:104. 1976. TYPE: U.S.A. Nebraska: Kearney Co., "Prairie", 13 Jun 1891, *P.A. Rydberg s.n.* (LECTOTYPE: NY!, selected by T. Barkley but first published here).

My concept of this taxon is essentially the same as that of Das (1976). It occurs in the drier, more northwestern regions of the broad distribution of *Onosmodium bejariense*. Var. *occidentale* appears to intergrade into the *bejariense* in northcentral Texas, central Oklahoma, western Arkansas, northern Missouri, Illinois, and Minnesota.

REPRESENTATIVE SPECIMENS: This variety, for the most part, is well-marked; in Texas, it is known only from Wichita and Tarrant counties (*cf.* discussion under var. *bejariense*).

DISTRIBUTION (Figure 2) AND ECOLOGY: Northcentral Texas westwards to Colorado, Montana, and Canada, eastwards to Illinois and Wisconsin, mostly silty-clay or sandy soils; flowering May-July.

ONOSMODIUM BEJARIENSE A. DC. VAR. SUBSETOSUM (Mack. & Bush) B.L. Turner, *comb. nov.* BASIONYM: *Onosmodium subsetosum* Mack. & Bush *ex* Small, *Fl. S.E. U.S.* 1001. 1903. *Onosmodium molle* Michx. var. *subsetosum* (Mack. & Bush) Cronquist, *Vasc. Pl. Pacific NW* 4:234. 1959. *Onosmodium molle* Michx. subsp. *subsetosum* (Mack. & Bush) Cochrane, Michigan Bot. 15:104. 1976. TYPE: U.S.A. Missouri: Barry Co.: near Eagle Rock, "Common barens", 11 Jul 1897, *B.F. Bush 135* (HOLOTYPE: MO!; Isotypes: GH!,US!).

Var. *subsetosum*, for the most part, is readily distinguished from related varietal taxa by its robust habit and glabrous lower stems. My evaluation of the taxon is essentially the same as that of Das (1965), both of us recognizing its intergradation into var. *occidentale*, as noted below. The taxon has a relatively well-defined distribution and does not co-occur with yet other varieties, although it appears to intergrade into the varieties *bejariense* and *occidentale* to the south and north respectively, and possibly var. *hispidissimum* to the east, but not markedly so. Indeed, were it not for the few "intermediates" cited below, the taxon would have been treated as a species.

REPRESENTATIVE SPECIMENS: Since the var. *subsetosum* is well-marked and, for the most part, does not co-occur with peripheral taxa, typical specimens are not cited. Two Missouri specimens thought to be "intermediate" with var. *bejariense* are cited here: Hempstead Co., *Palmer 8039* (MO); Izard Co., *Demaree 17022* (F). The former specimen is seemingly more or less intermediate, but the latter is more likely a pubescent-stemmed variant of an otherwise largely glabrous populational unit of typical *subsetosum*, this presumably the result of gene flow from its ancestral relative (presumably var. *bejariense*). It is noteworthy that label data on *Steyermark 73999* (F) calls attention to a population in Missouri (Cooper Co.) in which both hispid- and glabrous-stemmed plants occur, otherwise the plants concerned are typical of var. *subsetosum*.

DISTRIBUTION (Figure 4) AND ECOLOGY: Ozark highlands of Missouri and northern Arkansas (and closely adjacent Oklahoma) where it reportedly occurs in wooded limestone uplands and slopes in grassy glades; flowering May-June.

ONOSMODIUM DODRANTALE I.M. Johnst., J. Arnold Arb. 18:22. 1937. TYPE: MEXICO. Nuevo León: Mpio. de Galeana, Peak of Cerro Potosí,

"Scattered in colonies in the upper pine wood", 21 Jul 1935, *C.H. Mueller 2259* (HOLOTYPE: GH!; Isotypes: F!,GH!,MICH!,TEX!).

Stiffly erect perennial herbs 15-30 cm high. Stems rhizomatous, coarsely pilose with spreading or incurved hairs mostly 1-2 mm long. Midstem leaves ovate-elliptic, mostly 2-4 cm long, 0.8-1.3 cm wide, sessile or nearly so, moderately pubescent on both surfaces. Flowers arranged 3-10 in terminal leafy racemes, the pedicels mostly 3-10 mm long. Calyces 6-12 mm long, the lobes linear-lanceolate, 1-2 mm wide. Mature corollas yellow with greenish lobes; tubes 9-12 mm long, glabrous within; lobes deltoid, 3-4 mm long, the apices acute, sparsely pubescent to glabrous within, softly appressed-pubescent without, the glandular pleat 2-3 mm long, 0.1-0.5 mm high. Stamens extending to the base of lobes; anthers 2-3 mm long, the apical mucro ca. 0.1 mm long, recurved or not. Styles extending beyond the corollas for 4-16 mm, the apices bifid with globose stigmatic regions. Nutlets white, ca. 4 mm long, with a well-developed ventral ridge.

As noted by Johnston in his original description, this is a well-marked species easily recognized by its low stature and relatively simple vestiture.

SPECIMENS EXAMINED: MEXICO. Nuevo León: Peña Nevada, 26 mi NE of Dr. Arroyo, ca. 3300 m, 4 Jul 1959, *Beaman 2691* (GH); San Antonio Peña Nevada, 2740 m, 29 May 1978, *Hinton et al. 17378* (MEXU); Cerro Potosí, 3500 m, 21 Jun 1985, *McDonald 1566* (TEX); Cerro Potosí, 3500-3700 m, 26 Jul 1985, *McDonald 1808* (TEX,WIS); Cerro Potosí, 3550 m, 26 Jul 1985, *McDonald 1823* (TEX); Cerro Potosí, ca. 9000 ft, 8 Jul 1963, *McGregor et al. 290* (KANU); ascent of Infernillo, ca. 15 mi SW of Galeana, 9000-10000 ft, 29 Jun 1934, *Mueller 923* (F,GH,MICH,TEX); El Infernillo, 3000-3100, 29 Jun 1934, *Pennell 17116* (GH,PH). Tamaulipas: E side of Peña Nevada, 3500-3600 m, 5 Jul 1985, *McDonald 1651* (TEX); 7 km SW of Miquihuana, 3600 m, 5 Aug 1941, *Stanford et al. 909* (ARIZ,CAS-DS,GH).

DISTRIBUTION (Figure 6) AND ECOLOGY: Mountainous regions of southern Nuevo León and closely adjacent Tamaulipas, mostly in open pine forests, 3000-3600 m; flowering May-Aug.

ONOSMODIUM HELLERI Small, *Fl. Southeast. U.S.* 1000, 1337. 1908. TYPE: U.S.A. Texas: Kerr Co., along Bear Creek, 30 Apr 1894, *A.A. Heller 1682* (HOLOTYPE: NY!; Isotypes: UC!,US!).

Erect herbs mostly 35-60 cm high. Stems 1-several, arising from the crown of a ligneous or woody root, pubescent with both reflexed and spreading coarse hairs, the vestiture 1-2 mm high. Midstem leaves narrowly to broadly elliptic, mostly 8-16 cm long, (2-)3-8 cm wide, sparsely pilose on both surfaces, the hairs broad-based and rough to the touch. Flowers in terminal lax racemes, or

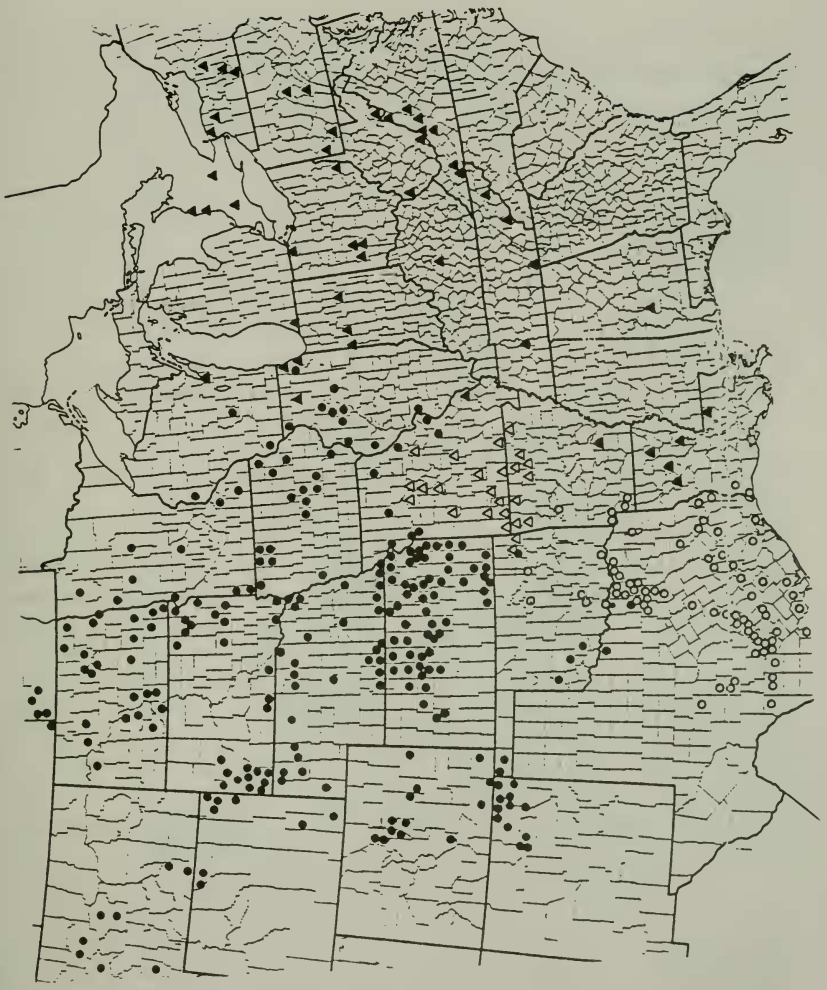


Figure 5: Site-map documenting the distribution of the varieties of *Onosmodium bejariense* from which Figures 1-4 were constructed: var. *bejariense* (open circles); var. *hispidissimum* (closed triangles); var. *occidentale* (closed circles); var. *subsetosum* (open triangles). Intergradants between these several taxa occur near their distributional boundaries, but for simplicity they are not shown by symbol here, but many of these were annotated as such and are on file in the herbaria concerned. The specimen from Utah was perhaps improperly labeled as to location.

Figure 6. Distribution of the Mexican species of *Onosmodium*: *O. dodrantale* (open circles); *O. oaxacanum* (closed triangles); and *O. unicum* (closed circles).

occasionally axillary; pedicels at maturity mostly 5-15 mm long. Calyces 6-10 mm long, the lobes linear-lanceolate, 1-2 mm wide. Larger corollas creamy-white; tubes 6-9 mm long, glabrous within; lobes deltoid, 3-4 mm long, the apices acute, sparsely pilose without, glabrous within, pleats seemingly absent. Stamens sagittate, extending ca. 1 mm beyond the base of the lobes, the filaments ca. 2 mm long, some of them markedly flattened and attached near the base; anthers ca. 2.5 mm long, the apical mucro ca. 0.2 mm long, recurved. Styles extending beyond the corollas for 6-12 mm, the apices bifid with globose stigmatic regions. Nutlets white, 3.0-3.6 mm long, 2.5-3.0 mm wide, mostly smooth, without basal constrictions.

This species has been recognized as distinct and well-marked by most workers, although acknowledged to be extremely variable in its vegetative characters, which appears to be the case. Das (1965) notes that "Intermediates between this variety (sic) and others seem to be rare. The only one noticed is the collection of *D. Demaree 20546* (SMU,MIN) from 'Mount Nebo State Park, Yell Co., Texas,' which resembles *O. molle* var. *subsetosum* in hair pattern on the upper surface of leaf." This must be a citation error or writing lapse, for the place cited is neither in Texas nor is the specimen intermediate. But Das concludes, correctly I think, that "In the absence of clear intermediates and from the fact that *O. helleri* maintains its distinctiveness though occurring with *O. molle* var. *bejariense*, it seems justifiable to continue to treat *O. helleri* as a distinct species."

Nevertheless, Johnston (1967) apparently had great difficulty in separating *Onosmodium helleri* from *O. bejariense*, to judge from his "strained" key to species in the publication concerned. Numerous collections of *O. helleri* have been made since these early studies and it now seems clear that *O. helleri* is a localized endemic of southcentral Texas largely confined to the juniper-oak woodlands along the Edwards Plateau where it characteristically occurs in rather bare crumbly limestone soils, usually on slopes. *Onosmodium bejariense* is a species of more open grassland habitats occurring in deeper soils.

REPRESENTATIVE SPECIMENS: U.S.A. Texas: Bandera Co.: *Cutler 872* (WIS). Bexar Co.: *Ripley 4141* (NY). Comal Co.: *Lindheimer 1025* (ARIZ,F,GH,NY,PH,TEX,UC,US). Hays Co.: *Kidder s.n.* (GH). Kendall Co.: *Correll 29578* (GH,LL,MICH,TEX,UC,US). Travis Co.: *Carr 4724, 6006, 9066, 9113, 9114, 10732, 10982* (all TEX).

ONOSMODIUM MOLLE Michx., *Fl. Bor. Amer.* 1:133. 1803. *Lithospermum molle* (Michx.) Muhl., *Cat.* 19. 1813. *Purshia mollis* (Michx.) Lehm., *Asperif.* 383. 1818. *Onosmodium carolinianum* L. var. *mollis* (Michx.) A. Gray, *Syn. Fl. N. Amer.* 2(1):206. 1878. TYPE: U.S.A. Tennesee: Davidson Co., Nashville, 1816, *Nuttall s.n.* (HOLOTYPE: PH, not examined).

This taxon is readily distinguished by a combination of characters, most notably by its ashy-grey relatively narrow leaves which are abundantly and uniformly appressed-strigose on both surfaces, small corollas (mostly 7-9 mm long) with mostly glabrous tubes and softly puberulent lobes. Furthermore, it is apparently endemic to the cedar glades of Tennessee and closely adjacent Kentucky and Alabama. In my opinion, it does not intergrade with any of the varieties of *Onosmodium bejariense*.

Das (1965) called attention to a number of geographically remote collections of *Onosmodium molle* which show a "faint look" of *O. bejariense* var. *occidentale* and specifically cited a collection from Hempstead Co., Arkansas, (*Palmer 839* [MO,US]) which he thought to be "intermediate between var. *occidentale* and [*O. molle*]"; my examination of the specimens concerned show these to be likely intermediates between varieties *bejariense* and *subsetosum* of *O. bejariense*, as their geography might suggest.

Onosmodium molle was reduced to a variety of *O. carolinianum* (= *O. virginianum*) by Gray but the latter's concept apparently included elements of *O. bejariense* var. *occidentale* and *O. bejariense* var. *bejariense*, although the description rendered is strictly that of *O. molle*. Johnston (1924) retained *O. molle*, but 30 years later, after considerable study of the group, he apparently felt that the taxon was "incapable of sharp definition" (Johnston 1954a, p. 20). Johnston specifically noted that "Embarrassingly transitional forms [between *O. molle* and *O. bejariense* var. *subsetosum*] appear to be frequent in Missouri, Iowa and Illinois where the ranges of the various species converge or even overlap. Analysis will probably reveal evidence of much hybridization and intragression (sic) affecting *O. hispidissimum*, *O. occidentale*, and *O. molle* in that area". In truth, the region called to the fore by Johnston is a region of populational intergradation between the varieties *hispidissimum* and *occidentale* of *Onosmodium bejariense*, probably having little to do with hybridization *per se*, but rather reflects the sorting out of the more western, less hispidulous, larger-flowered populations (var. *occidentale*) from the eastern, more hispidulous, smaller-flowered populations (var. *hispidissimum*). In this region (even within a single county, *e.g.*, Peoria Co., Illinois) numerous intermediates between these two varietal taxa occur (much commented upon by several floristic workers, and by Das 1965), and the occasional variant in this region might be expected to approach *O. molle* in this or that character, which I take to be the cause for the citation by Das of a collection of *O. molle* from Jackson Co., Illinois (*Gleason 2578* [GH]), the only collection of the latter thought by Das to occur outside of its "cedar glades" habitat.

As noted above, *Onosmodium molle* is confined to cedar glade habitats of central Tennessee and closely adjacent states, and it is the most often collected taxon of *Onosmodium* in that state. I have examined only a few collections of *O. bejariense* var. *hispidissimum* from Tennessee (Figure 3), one of these from Marion County (*Webb 5029* [GH]), the latter adjacent to Franklin County,

Tennessee, where *O. molle* is known to occur. Perhaps these two taxa will be found growing together in this latter region, with the occasional hybrid, but the herbarium material I have examined strongly suggests that two distinct taxa are involved. At least I saw no clear intermediates.

Regardless of its nomenclatural treatment, it seems apparent to me that *Onosmodium molle* is a more cohesive, more clearly defined taxonomic entity than are the several varieties of *O. bejariense*, all of which intergrade to some considerable extent in their regions of peripheral contact. This does not appear to be the case with *O. molle*, hence its recognition as a species here.

After the above was written I happened upon a detailed paper by Kral (1983) in which he took essentially the same view as I have expressed here, noting that *Onosmodium molle* is a calciphilic endemic occurring "usually in pure populations within its narrow range", but noting that it is sympatric with what I consider *O. bejariense* var. *hispidissimum*. Apparently, he too did not find intergrades between these taxa; at least these were not commented upon. My Figure 8, showing the distribution of *O. molle*, has been enhanced by two collections from northwestern Alabama mapped by Kral, collections which I did not examine.

REPRESENTATIVE SPECIMENS: U.S.A. Kentucky: Logan Co.: *Palmer 17745* (MO). Tennessee: Davidson Co.: *Chofin s.n.* (KANU); *Kral 30533* (MICH); *Eggleston 4446* (MO); *Gattinger 2100* (F,NY); *Shanks 1535* (UC). Franklin Co.: *Wofford 86-50* (GH). Maury Co.: *Kral 26735* (KANU,OKLA). Rutherford Co.: *Kral 31017* (MICH); *McGregor 17164* (KANU). Wilson Co.: *Kral 26971* (KANU).

ONOSMODIUM OAXACANUM B.L. Turner, *sp. nov.* TYPE: MEXICO. Oaxaca: Llano Udadi, 4 km SE of San Andreas Lagunas, *Pinus pseudostrobus* woodland, 2380 m, 10 Jul 1981, *A. Garcia M. 504* (HOLOTYPE: MEXU!).

Onosmodio dodrantali I.M. Johnston similis sed foliis multo majoribus (5-10 cm longis vs. 2-4 cm longis), floribus numerosioribus (20-40 vs. 3-10) in racemis circinatis, et corollis intus pubescentibus (vs. glabris) differt.

Stiffly erect perennial herbs 27-40 cm high. Stems arising from a thick ligneous rootstock, moderately long-pilose, the hairs 2-3 mm long and of only 1 kind. Midstem leaves lanceolate-elliptic to oblanceolate, mostly 5-10 cm long, 1.0-1.3 cm wide, sessile and somewhat clasping, about equally pilose on both surfaces with broad-based hairs. Flowers numerous (20-40) and densely arranged in terminal bracteate circinnate racemes (sometimes 2 racemes terminating a stem), the pedicels mostly 3-10 mm long (in fruit). Calyces 10-13

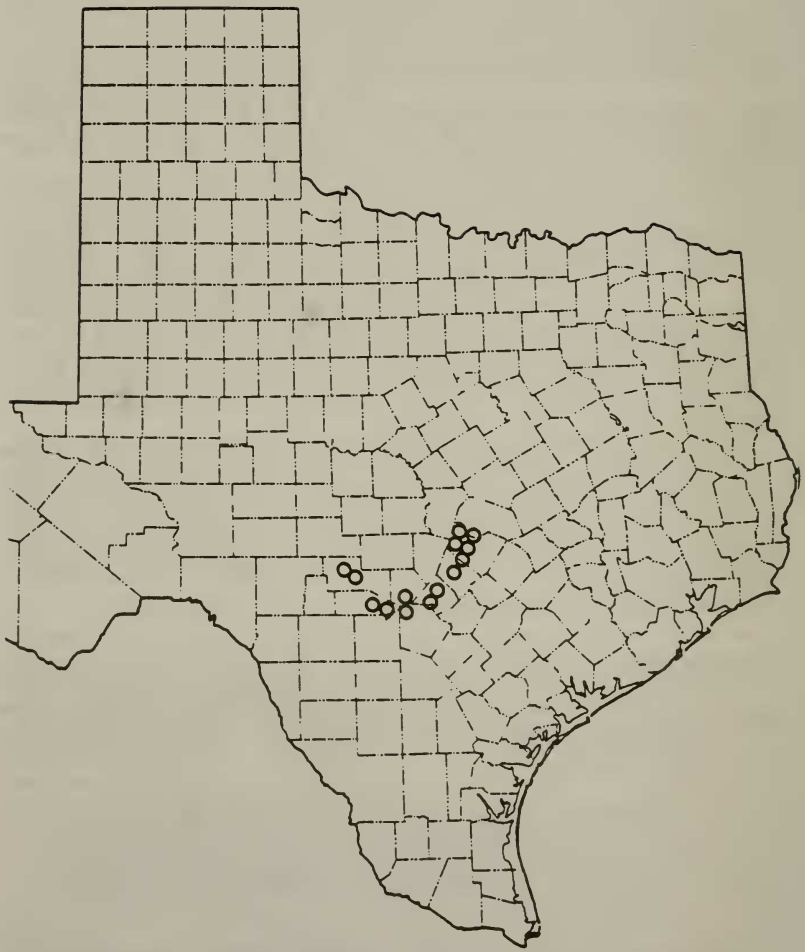


Figure 7. Distribution of *Onosmodium helleri* (open circles).

Figure 8. Distribution of *Onosmodium bejariense* var. *subsetosum* (open circles), and *O. molle* (closed circles).

mm long, the lobes linear-lanceolate 1.2-2.7 mm wide. Larger corollas yellow with greenish lobes; tubes 8-10 mm long, sparsely pubescent within, especially the lower portion, the hairs to 1 mm long; lobes narrowly deltoid, 2.5-3.0 mm long, 1.5-2.0 mm wide, the outer surfaces densely sericeous, the inner surfaces glabrous or nearly so, except near the apices, the pleats poorly developed, if at all. Stamens extending to the base of corolla lobes; anthers ca. 2.3 mm long, joined to the filament ca. 1/3 from its base, glabrous, the apical mucro much-reduced, ca. 0.1 mm long. Nutlets decidedly greyish, ca. 4 mm long, 3 mm wide, the inner ridge sharp, ca. 2 mm long.

This is a very distinctive taxon, seemingly most closely related to *Onosmodium dodrantale* but readily distinguished by its large leaves, more numerous-flowered bracteate racemes, and corollas with interior portion markedly pubescent.

ADDITIONAL SPECIMEN EXAMINED: MEXICO. Oaxaca: 4 km al N de Guadalupe Tixa, sobre el camino a San Andres Laguna, Distr. Teposcolula, pine forest, 2260 m, 15 Jul 1986, *Garcia M. 2657* (MEXU).

DISTRIBUTION (Figure 6) AND ECOLOGY: Known only from Oaxaca where it is reported "abundante" in open areas of pine forests, 2200-2400 m; flowering July.

ONOSMODIUM UNICUM Macbride, Contr. Gray Herb. n.s. 49:21. 1917. TYPE: MEXICO. San Luis Potosí: Alvarez, 13-23 Jul 1904, *E. Palmer 185* (HOLOTYPE: GH!; Isotype: F!).

Stiffly erect much-branched perennial herbs 40-60 cm high. Stems from thick ligneous rootstocks, pubescent with both appressed and spreading coarse hairs, distributed among these to varying degrees an array of delicate multi-septate glandular trichomes, 0.3-0.8 mm long. Midstem leaves (of primary stems) mostly lanceolate-ovate, 5-9 cm long 1-2 cm wide, sessile or nearly so, sparsely to densely appressed-pubescent on both surfaces. Flowers 10 or more arranged in terminal leafy racemes 10-30 cm long, the pedicels mostly 5-15 mm long. Calyces mostly 7-10 mm long, the lobes linear-lanceolate, 2-4 mm long, 1.0-1.5 mm wide. Larger corollas yellow with greenish lobes; tubes 9-11 mm long, glabrous within; lobes narrowly deltoid, 2-4 mm long, the apices acute, appressed-pubescent without, glabrous within, the pleats inconspicuous. Stamens extending to the base of corolla lobes; anthers ca. 3.5 mm long, the apical mucro ca. 0.3 mm long, recurved. Styles extending beyond the corollas for 5-10 mm, the apices bifid. Nutlets beige, ca. 4 mm long, 2-3 mm wide, basally flanged, the dorsal ridge confined to the upper half.

Johnston (1954a) remarked that *Onosmodium unicum* was "scarcely more than a pubescent geographic form of *O. bejariense* and perhaps does not merit specific rank." The taxon was known to him only by type material. Since that

time numerous collections of the species have been made over a large area and it seems clearly worthy of recognition. Das (1965) also recognized the species, noting its distinctive glandular vestiture.

REPRESENTATIVE SPECIMENS: MEXICO. Nuevo León: Dulces Nombres, 1800 m, 14 Jul 1948, *Meyer & Rogers 2775* (GH). Querétaro: 2 km N of San Joaquín, 2300 m, 26 Sep 1991, *Fernández 4800* (MEXU). San Luis Potosí: Alvarez, 2200-2400 m, 30-31 Jul 1934, *Pennell 17861* (GH,PH). Hidalgo: Zimapan, upper end of Barranca de San Vicinte, 2000 m, 25 Sep 1946, *Moore 1303* (GH); between Zacualtipán and Olotla, 3 Jul 1947, *Moore 3271* (GH,UC); 13.5 mi by road SW of Jacala, 11 Jun 1962, *Webster et al. 11319* (F,MEXU). Tamaulipas: ca. 2 km N of Julio, Sierra de Guatemala, 1600 m, 19-25 Aug 1984, *Johnston 12828* (TEX).

DISTRIBUTION (Figure 6) AND ECOLOGY: Nuevo León, Tamaulipas, San Luis Potosí, Querétaro, and Hidalgo, mostly in pine-oak woodland from 1600-2300 m; flowering May-August.

ONOSMODIUM VIRGINIANUM (L.) A.DC., *Prodr.* 10:70. 1846. BASIONYM: *Lithospermum virginianum* L., *Sp. Pl.* 1:132. 1753. ≡ *Onosmodium hispidum* Michx., *Fl. Bor. Amer.* 1:133. 1803. TYPE: U.S.A. Virginia: w/o specific locality, date, or collector (HOLOTYPE: L; not examined).

Onosmodium virginianum (L.) A.DC. var. *hirsutum* Mack., Bull. Torrey Bot. Club 32:499. 1905. TYPE: U.S.A. Alabama: Lee Co., Auburn, 29 May 1897, *Earle & Baker s.n.* (HOLOTYPE: MO, not examined).

Onosmodium alabamense Gand., Bull. Soc. Bot. France 65:63. 1918. TYPE: U.S.A. Alabama: "Gateswood", 1 May 1903, *S.M. Tracy 8400* (HOLOTYPE: P; Isotype: GH!).

Onosmodium floridanum Gand., Bull. Soc. Bot. France 65:63. 1918. TYPE: U.S.A. Florida: Polk Co.: *Ohlinger 618* (HOLOTYPE: P).

Onosmodium longistylum Gand., Bull. Soc. Bot. France 65:63. 1918. TYPE: U.S.A. South Carolina: Oconee Co.[?]: about "Oconec", without date, *Anderson s.n.* (HOLOTYPE: P).

Erect perennial herbs mostly 30-45 mm high. Stems rhizomatous, strigose, the hairs mostly appressed (except for forms from the southeastern U.S.A. with spreading hairs which have been given the name var. *hirsutum*), mostly 0.5-1.1 mm long. Midstem leaves mostly oblanceolate, 5-8 cm long, 1.2-2.0 cm wide, sessile to subpetiolate, pubescent like the stems except for the occasional ascending hairs along the veins. Flowers arranged 10-40 in branched terminal

racemes, the branches 6-14 cm long at anthesis, the pedicels 1-3 mm long. Calyces 4-7 mm long, the lobes linear-lanceolate, 2-3 mm long, 0.6-1.4 mm wide. Larger corollas 8-14 mm long, decidedly yellowish; tubes 6-9 mm long; lobes narrowly linear, mostly 3-5 mm long, 1.0-1.2 mm wide, 3-4 times as long as wide, sparsely pubescent within and without. Stamens extending to base of the corolla lobes; anthers 2-3 mm long, including the apical mucro. Mature styles extending beyond the corollas for 5-10 mm, the apices weakly bifid with globose stigmatic areas. Nutlets white to somewhat brownish apically, 2.5-3.0 mm long, 1.5-2.0 mm wide, without a basal flange.

While quite variable, this is a fairly clear-cut taxon with a distinct distribution (Figure 9), although Gray, early on, included *Onosmodium molle* within its parameters. I noted no clear intermediates between *O. virginianum* and other taxa. Populational forms with spreading hairs are commonly encountered from eastern Louisiana to Florida. These have been referred to as *O. virginianum* var. *hirsutum* by some workers, but such forms often occur within the same general region as the more typical forms (*e.g.*, in Polk Co., Florida). Since the hirsute forms do not appear to differ otherwise from typical forms of *O. virginianum*, formal taxonomic status seems superfluous.

REPRESENTATIVE SPECIMENS: Specimens are not cited here since the species is represented by numerous collections throughout the region concerned, there being little argument as to their identity, except for collections from the southeastern portion of its range where ancestral introgression from *Onosmodium bejariense* may have occurred.

DISTRIBUTION (Figure 9) AND ECOLOGY: Mostly occurring in light sandy soils in openings or cleared areas of pine-oak forests of the Atlantic and Gulf Coastal Regions; flowering May-Aug.

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Figure 9. Distribution of *Onosmodium virginianum* (closed circles).

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